ECOLOGICAL STUDIES OF MICROARTHROPODS IN FOREST SOILS, WITH EMPHASIS ON RELATIONS TO SOIL ACIDITY

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CONTENTS

I. PREFACE

The present work was performed mainly within the framework of the »SNSF-project» (»Acid precipitation - effects on forest and fish»). In 1981 the studies were incorporated in a project entitled »Effects of acid precipitation on forest and soil». Financial support was given by the Agricultural Research Council of Norway, and to some degree also by the Norwegian Forest Research Institute, where the work was carried out.

I want to thank the staff of the two divisions in which I have worked (Division of Forest Protection and Division of Forest Ecology) for their help and friendship. The heads of these divisions, Professor, dr. philos Alf Bakke and Professor, dr. agric Kristian Bjor are heartily thanked for their support and encouragement. Among my collaborators, it is a pleasure to acknowledge my three co-authors (dr. agric Gunnar Abrahamsen, Terje Amundsen and Bjørn Kjøndal) for fruitful cooperation. Dr. Abrahamsen is especially thanked for his conscientious reading of all manuscripts, his constructive criticism, and good advice during the work.

Ås, February 1984 Sigmund Hågvar

II. INTRODUCTION

Both in Europe and North America, long-range transported air pollutants have markedly increased the acidity of rain and snow during the latter decades (Dovland et al. 1976, Anon. 1977, Likens et al. 1979). The Norwegian »SNSF-project» was initiated to study possible effects of acid precipitation on forest and fish (Overrein et al. 1980). In forest, the project concentrated upon processes wich influence tree growth. Soil animals were included since they participate in decomposition processes which regulate the availability of plant nutrients. Especially in the poorer coniferous forests, which are common in Norway, a large part of the nutrient pool may be situated in the layers of slowly decomposing raw humus.

The role of soil animals in the decomposition pathways is still poorly known. Changes in soil animal communities are therefore difficult to interpret in terms of plant nutrient availability. However, the extensive field experiments originally designed for measuring effects on decomposition rates, soil chemistry and tree growth (Abrahamsen et al. 1976) represented a unique opportunity for studying relations between soil acidity and soil fauna. The present study deals mainly with microarthropods (Acari and Collembola), which are very abundant in coniferous forest soils. The field experiments were supplemented by laboratory experiments under more controlled conditions. A general need for a better understanding of the ecology of these animals also initiated studies wich were not directly related to the acidification problems.

Counting and identification of soil animals is a very time-consuming work, and taxonomical problems often arise. Initially, my work was limited to Collembola. However, through cooperation with the co-authors, the study was extended to Acari, and in one paper also to Enchytraeidae. This allowed for interesting comparisons between different animal groups.

III LIST OF PAPERS

1. Hågvar, S. and Abrahamsen, G. 1980. Colonisation by Enchytraeidae, Collembola and Acari in sterile soil samples with adjusted pH levels. Oikos 34: 245–258.
2. Hågvar, S. and Amundsen, T. 1981. Effects of liming and artificial acid rain on the mite (Acari) fauna in coniferous forest. Oikos 37: 7–20.
3. Hågvar, S. (manuscript). Effects of liming and artificial acid rain on Collembola and Protura in coniferous forest. Submitted.
4. Hågvar, S. and Kjøndal, B.R. 1981. Decomposition of birch leaves: dry weight loss, chemical changes, and effects of artificial acid rain. Pedobiologia 22: 232–245.

5. Hågvar, S. and Kjøndal, B.R. 1981. Succession, diversity and feeding habits of microarthropods in decomposing birch leaves. Pedobiologia 22: 385–408.

6. Hågvar, S. and Kjøndal, B.R. 1981. Effects of artificial acid rain on the microarthropod fauna in decomposing birch leaves. Pedobiologia 22: 409–422.

7. Hågvar, S. 1982. Collembola in Norwegian coniferous forest soils I. Relations to plant communities and soil fertility. Pedobiologia 24: 255–296.

8. Hågvar, S. 1983. Collembola in Norwegian coniferous forest soils II. Vertical distribution. Pedobiologia 25: 383–401.

9. Hågvar, S. and Abrahamsen, G. (manuscript). Collembola in Norwegian coniferous forest soils III. Relations to soil chemistry. Submitted.

10. Hågvar, S. (manuscript). Six common mite species (Acari) in Norwegian coniferous forest soils: Relations to vegetation types and soil characteristics. Submitted.

IV. CORRECTIONS AND ADDITIONS

Paper 1.

p. 249, column 1, line 5: Instead of »90.0% = 0.6», read »90.0% ± 0.6».
» » » » » 11: » » »Fridericia», read »Fredericia».
» » » » » 11: » » »bucholzi», read »buchholzi».
» » » » » 14: » » »Fridericia», read »Fredericia».
» 254, » » » 8: » » »S. nova», read »S. cf. nova».
» 257, » » » 7: » » »non-significant», read »significant».
» 258, » » » 12: Add to »Toxicol.» : »23:737–740.

Paper 2.

p. 13, column 1, line 2: Instead of »increases», read »increased».

Paper 4.

p. 241, line 15: Instead of »ATTIWAILL», read »ATTIWILL».
» 242, » 7 in chapter 5: Instead of »discquilibrium», read »disequilibrium».

Paper 5.

p. 398, line 27: Instead of »were all were», read »were all».

Paper 6.

p. 410, line 10: Instead of »with for», read »with four».
» 411, » 1: » » »Effect artificial», read »Effect of artificial».
» 420, » 31: » » »restris», read »vestris».
» 422, » 16 from below: Instead of »KØNDAL», read »KJØNDAL».
» » » » » »: » » »habitats», read »habits».

Paper 7.

p. 264, line 8 in chapter 3.4: Instead of »which and different», read »which had a different».
» 266, » 1: Instead of » = », read » ⩾ ».
» 285, » 23: » » »last», read »list».
» 295, » 7: » » »MACFAYDEN», read »MACFADYEN».
» » lowest line: Instead of »Postbox 6», read »Postbox 61».

Paper 8.

p. 385, line 18–19: Instead of »Loss on ignation», read »Loss on ignition».
» 399, » 13: » » »l'axception», read »l'exception».

V. SUMMARIES AND DISCUSSION

1. Classification of the papers

The papers fall into two main groups: those which concern relationships between microarthropods and soil acidity (papers 1, 2, 3, 4, 6, 9 and 10), and those which illuminate other aspects of microarthropod ecology (papers 5, 7, and 8). Some of the papers in the first group also contain aspects beyond the realm of soil acidity. Paper 4 treats the effects of artificial acid rain on the dry weight loss and chemistry of birch leaves. The paper has been included because it describes the environmental conditions of the microarthropod fauna treated in paper 6.

The leading question in the first category of papers has been: »Are there relationships between the microarthropod fauna and soil acidity?» This question has been studied by examining:

A. The ability to colonise sterile soil samples of different pH.

B. Reactions to artificial pH changes in podzol soil (Typic Udipsamment) and decomposing birch leaves.

C. The distribution of microarthropod species in natural soils of different pH. This was considered to be an important control of the experimental results. If a general relationship exists between soil pH and the abundance of a given species, this should also be reflected under natural field conditions.

The papers dealing with microarthropods and soil pH have been classified below, according to methodological approach (Table 1).

Table 1. Classification of papers dealing with microarthropods and soil pH, according to methodological approach. The number and a few key words of each paper is given.

A. Colonisation experiment	B. Experimental acidification and liming	C. Occurrence in natural soils of different pH
1. Colonisation of sterile soil of different pH (Acari and Collembola)	2. Field experiments, coniferous forest soil (Acari)	9. Collembola related to soil chemistry
	3. As above (Collembola)	10. Acari (selected species) related to soil chemistry
	6. Field and laboratory experiments with decomposing birch leaves (Acari and Collembola)	
	4. Chemistry of leaves used as substrate in no. 6.	

Three papers deal with aspects of microarthropod ecology other than those mentioned in Table 1. Paper 5 describes the succession, diversity and feeding habits of microarthropods in decomposing birch leaves. Papers 7 and 8 analyse the Collembola fauna in coniferous forest soils: first the relations to plant communities and soil fertility, and then the vertical distribution. Selected species of Acari have also been analyzed for these aspects in paper 10.

2. Microarthropods and soil acidity

Abstracts of the seven relevant papers are given below, followed by a discussion of the results.

2.1. Abstracts

Paper 1. Colonisation by Enchytraeidae, Collembola and Acari in sterile soil samples with adjusted pH levels.

Soil animals were allowed to colonise sterile soil samples from three soil types: raw humus, poor mull and rich mull. Within each soil type, samples adjusted to three different pH levels were offered. Soil pH significantly influenced the success of colonisation in the following number of species: Collembola 7, Oribatei 8 (minimum), Mesostigmata 3, Astigmata 1, Enchytraeidae 3, and Lumbricidae 1. In all three soils, there were reactions both in favour of acidification and of liming. The largest number of species reacting to the treatments was found in raw humus, where the most marked pH gradient occurred. When a species reacted to both lowered and raised soil pH, these reactions were always opposite. Within the same species, reaction patterns in different soil types supported each other. High numbers of Acari in acidified raw humus was mainly due to *Tectocepheus velatus* Michael, *Nothrus silvestris* Nicolet and *Schwiebea* cf. *nova* (Oudemans). Age structure indicated that soil pH influenced reproductive success. For several species, reactions were supported by current field experiments and information on the species' natural occurrence.

Paper 2. Effects of liming and artificial acid rain on the mite (Acari) fauna in coniferous forest.

Both increased soil acidity induced by artificial acid »rain» (diluted sulphuric acid), and lowered soil acidity after liming ($CaCO_3$), influenced the abundance of several species and groups of Acari. Liming reduced the abundance of various Oribatei (*Tectocepheus velatus, Nothrus silvestris, Nanhermannia* sp., *Brachychochthonius zelawaiensis*), the Gamasina species *Parazercon sarekensis,* as well as total Oribatei, total Mesostigmata, and total Acari. *Trachytes* sp., however, increased on limed plots. Acidification gave increased abundance of *T. velatus* and »Brachychthoniidae except *B. zelawaiensis*», while the abundance of *P. sarekensis, Trachytes* sp., total Mesostigmata, total Prostigmata and total Acari decreased. Generally, increased soil acidity gave higher dominance of Oribatei. Liming, and to a smaller degree acidification, changed the vertical distribution pattern in Oribatei, giving a higher percentage in the A_e layer (3–6 cm) compared to the O layer (0–3 cm). However, in Prostigmata, liming resulted in an increased percentage in the O layer compared to the A_e layer. The observed results cannot be explained in relation to predation pressure by the larger Gamasina, nor to the amount of fungal hyphae. It is suggested that reproduction success in several species is related to soil pH.

Paper 3. Effects of liming and artificial acid rain on Collembola and Protura in coniferous forest.

In coniferous forest with podzol soil, field experiments were performed with liming ($CaCO_3$) and artificial acid rain (diluted sulphuric acid, strongest treatment pH 2).

Increased soil pH after liming reduced the abundance of several collembolan species. In two of three experiments, the total abundance of Collembola was significantly reduced. The abundance of Protura increased in one experiment.

Reduced soil pH (mainly after application of water with pH 2–2.5) resulted in a complex reaction pattern. Increased abundance was observed in *Mesaphorura yosii, Karlstejnia norvegica* and *Willemia anophthalma.* Total Collembola numbers increased in one site. Among the species which declined under acidification, the most marked reduction was in *Isotoma notabilis*.

The vertical distribution of Collembola was affected both by liming (two species) and acidification (five species and total Collembola). All changes involved an increased percentage in the 3–6 cm layer (E, eluvial layer) compared to the 0–3 cm layer (0, raw humus).

Neither the amounts of fungal hyphae nor predation pressure by the larger Gamasina mites can explain the results. Competition is suggested as an important population regulating factor.

Paper 4. Decomposition of birch leaves: dry weight loss, chemical changes, and effects of artificial acid rain.

Leaves of birch (mixture of *Betula pubescens* EHRH. and *B. verrucosa* EHRH.) were kept in litter bags under small *B. verrucosa* plants (0.5–1m) on a previously clear-cut area. As much as 13% dry weight was lost during the first winter, when the ground was mostly covered by snow. After over three years, however, dry weight loss was not more than 37%. A corresponding weight loss occurred during only three months under warm and moist conditions in a similar greenhouse experiment. In the field, elements were lost at different rates (in % of initial weight): K > P > Mg > Ca > S > Mn > N. The total amount of N increased in litter bags after 1–3 years. Litter bags

both in the field and in a greenhouse were acidified with artificial acid »rain» (diluted sulphuric acid) of *p*H 4, 3 and 2. Application of ground water (*p*H 6) in the field and simulated »rain» (*p*H 5.3) in the greenhouse were considered as controls. The strongest acidification (*p*H 2) resulted in significantly lower decomposition rate in the »early» decomposition phase in the greenhouse. Corresponding tendencies were observed in a »late» decomposition phase in the greenhouse and in the field experiment. Application of *p*H 2-water also increased the leaching rate of Ca, Mg and Mn in both field and greenhouse experiments. Watering with a weaker acid (*p*H 3) did not affect decomposition rate or leaf chemstry significantly, except for increased leaching of Mn in the field. No effects could be observed from the *p*H 4-treatment.

Paper 6. Effects of artificial acid rain on the microarthropod fauna in decomposing birch leaves.

In a field experiment, artificial »rain» of *p*H 6, 4, 3 and 2 was applied to birch leaf litter (mixture of *Betula pubescens* EHRH. and *B. verrucosa* EHRH.) kept in litter bags with 1 mm mesh size. Fifty mm artificial »rain» was given once monthly in the frost-free period of the year (May–September), and the experiment was extended over more than three years. The various *p*H values were achieved by adding sulphuric acid to ground water (*p*H 6). Because the habitat (a clear-cut area) was rather warm and dry during summer time, less than 40% dry weight was lost during the whole study period. At the end of the experiment, significant effects of acidification were found among Oribatei, Mesostigmata and Collembola. In the most strongly acidified bags, the abundance of Oribatei had increased significantly. This was mainly due to a marked increase in the numbers of Brachychthoniidae [mainly *Brachychochthonius zelawaiensis* (SELLN.)] and *Tectocepheus velatus* (MICH.). Increased abundance on plots given *p*H 2-water was also noted for *Leioseius bicolor* (BERL.) [Mesostigmata] and *Neanura muscorum* (TEMPLETON) [Collembola]. However, reduced abundance was recorded among two Collembola species: *Isotoma notabilis* SCHÄFFER and *Lepidocyrtus cyaneus* TULLBERG.

A similar experiment was run for three months in a greenhouse, using both leaves in an »early» decomposition phase, and leaves in a »late» phase. Watering was performed frequently, with 10 mm twice a week, and natural precipitation was excluded. The frequent application with *p*H 2-water over this comparatively short time strongly reduced the total abundance of Collembola in both decomposition phases. In

the »late» phase, the reduction was significant also at the *p*H 3-treatment. All effects on single Collembola species were reductions. Several species of Mesostigmata seemed to achieve highest abundance at the *p*H 4- and *p*H 3-treatments in the »early» phase, while all reactions to acidification in the »late» phase were reductions (at the *p*H 2-level). Acidification did not affect the total abundance of Oribatei, but most reactions were reductions. However, in *Tectocepheus velatus* and *Steganacarus* spp., the abundance increased in both phases. Thus, the results revealed complicated reaction patterns, with great effect of the frequency of acid »rain» application. The field results are in accordance with other field studies and also a »preference» experiment, while the results from the greenhouse experiment have largely the character of »shock-effects».

Paper 9. Collembola in Norwegian coniferous forest soils. III. Relations to soil chemistry.

In 25 Collembola species, relationships between abundance and soil chemical properties were studied by analyses of correlation coefficients. Samples were taken from seven different vegetation types in each of two study areas, and the soils ranged from poor podzols to rich brown earth. Soil chemical properties were N, pH, base saturation %, exchangeable Ca, Mg, Mn, Na, K and loss on ignition. In each species, relationships were tested eight times, as samples were taken both in spring and autumn, in two depth levels (0–3 and 3–6 cm) and in two study areas. No species was significantly correlated to a given parameter more than four of these times (most often 1–3 times). Seven species repeated certain relationships in both study areas. The highest number of significant correlations were with pH, base saturation, Ca, Mg and Mn. These parameters increase with increasing soil fertility. A number of species characteristic for poor raw humus soils were negatively correlated to these properties, while certain »rich soil species» were positively correlated. Collembola species are relatively poor indicators of soil chemistry. Combinations of species may, however, improve the level of precision.

Paper 10. Six common mite species (Acari) in Norwegian coniferous forest soils: Relations to vegetation types and soil characteristics.

In each of two study areas, the abundances of six common mite species were studied in seven different vegetation types of coniferous forest. Samples were taken in the 0–3 cm and 3–6 cm layers in spring and autumn. Three species belonged to Oribatei (*Tectocepheus*

velatus, Nothrus silvestris and *Brachychochthonius zelawaiensis*), two belonged to Astigmata (*Schwiebea* cf. *nova* and *S.* cf. *cavernicola*), and one to Mesostigmata (*Parazercon sarekensis*).

The three Oribatei species and *S.* cf. *nova* occurred mainly in poor and acidic podzol soils with raw humus. This finding conforms with the results from earlier acidification and liming experiments, in which these four species showed and »acidophilic» character. The two other species were also found abundantly in a poor brown earth soil, while none of the six species were abundant in rich brown earth sites with mull humus. Correlation to soil chemical parameters were carried out by using Spearman's rank correlation coefficient.

All species showed large variations in depth distribution, both between habitats and seasons. On the average, the following percentages of the populations occurred in the upper 3 cm: 85% in *T. velatus*, 65% in *P. sarekensis*, 60% in *S.* cf. *cavernicola*, 54% in *B. zelawaiensis*, 52% in *N. silvestris* and 51% in *S.* cf. *nova*.

2.2. General conclusions

To facilitate the discussion, all significant reactions to artificial acidification or liming have been collected in Table 2. For comparison, the table also includes the results from a Finnish liming experiment (Huhta et al. 1983) and a Swedish acidification experiment (Bååth et al. 1980).

The following conclusions can be drawn from Table 2:

1. Changes in soil pH have affected the abundance of a large number of species, both among Collembola and Acari.

2. Within both groups, several different reaction patterns appeared. The total picture thus becomes very complex. The results illustrate well the necessity of identifying the animals to species level.

3. Results from independent experiments did in most cases support each other for a given species.

4. Some species were especially sensitive to changes in soil acidity and showed significant reactions in several experiments. A number of species reacted in only one or a few experiments, while certain microarthropods (not included in the table) were never significantly affected.

5. The reactions can be classified into four categories:

   a) Abundance increased by acidification and/or reduced by liming.

   b) Abundance reduced by acidification and/or increased by liming.

   c) Abundance reduced by both acidification and liming.

   d) Various reactions (inconsistent reactions noted to either liming or acidification).

6. Most species belonged to categories 5a or 5b. Category 5a contains slightly more species than 5b. No species increased their abundance in both limed and acidified soil.

7. While a number of both Collembola and Acari species increased their abundance in certain acidification experiments, liming very rarely gave increased abundance of a species or group. A large number of microarthropod species reduced their abundance in limed soil.

8. When significant reactions to liming were noted in Collembola or Acari as a whole, the result was reduced abundance. Acidification could either reduce or increase the abundance of these groups. Significant reactions in Oribatei as a whole always implied reduced abundance in limed soil and increased abundance in acidified soil.

The Finnish and Swedish results conform well with the present data. The Swedish »*Tullbergia krausbaueri*» may prove to be identical with *Mesaphorura yosii*.

The many cases of reduced abundance in the greenhouse experiment (paper 6) are probably related to the frequent application of a strongly acidic solution (pH 2). For several species, the reactions may have had the character of »shock-effects». The following species of category four in Table 2 are therefore closely related to the first category: *Brachychochthonius zelawaiensis*, total Brachychthoniidae, and *Oppiella nova*. Most remaining taxa in the last category consist of species groups, which may explain the different reactions in different experiments.

2.3. Sensitive species

As noted in pt. 4 above, certain species seem to be especially sensitive to changes in soil acidity. Their significant reactions noted in Table 2 were often supported by non-significant trends. The following species should be especially considered:

Table 2. Significant reactions (P≤0.05) among microarthropods to artificial liming and acidification. The symbols + or - indicate increased or decreased abundance compared to control. Symbols in brackets mean that the difference is significant only when limed and acidified samples are compared. If not otherwise indicated, abundance data from field experiments are from the upper 6 cm (O+E), and the effects are related to the strongest treatment. All Collembola values include both adults and juveniles. Results from two foreign studies have been included in the table.

	EFFECT OF LIMING							EFFECT OF ACIDIFICATION									
Paper no.	1			2 and 3				1			2 and 3			6			
Experiment	Colonisation experiment			Field experiment			Huhta et al.	Colonisation experiment			Field experiment			Birch leaves Field	Birch leaves Green-house		Bååth et al.
Additional information	Raw humus	Poor mull	Rich mull	A-1 1975	A-1 1977	A-3 1978	1983	Raw humus	Poor mull	Rich mull	A-2 1975	A-2 1977	A-3 1978		Early decomp.	Late decomp.	1980
1. Increased abundance by acidification and/or reduced abundance by liming.																	
ACARI																	
Oribatei																	
Tectocepheus velatus (Michael), ad. + juv.	-					-	-9)	+	+				+	+	+	+	+5)
Nothrus silvestris Nicolet, ad. + juv.	-		(-)	-	-	-1)	-9)	+	+	(+)							
Steganacarus sp. ad.															+	+	
Nanhermannia sp. ad.				-													
Ceratozetes thienemanni (Willmann), ad.	-																
C. gracilis (Michael), ad.							-										
Oribatei, total						-	-9)	+			+2)		+1)	+			
Astigmata																	
Schwiebea cf. *nova* Vitzthum, ad. + juv.			(-)					+	+	(+)					+		
Astigmata, total								+	+	+					+		
Mesostigmata																	
Evíphis ostrinus (Koch), ad. + juv.															+		
Leioseius bicolor (Berlese), ad.														+			
COLLEMBOLA																	
Mesaphorura yosii Rusek					-	-	-	+			+	+4)					
Anurida pygmaea (Börner)	(-)					-	-	(+)									+5)
Willemia anophthalma Börner				-							+6)		+7)				
Karlstejnia norvegica Fjellberg													+7)				
Tullbergia krausbaueri s.l. Börner																	+
Folsomia sensibilis Kseneman						-											
F. fimetarioides (Axelson)							-										
Anurophorus septentrionalis Palissa						-											
Neanura muscorum (Templeton)														+			

Continues ÷

÷ Continued

	EFFECT OF LIMING							EFFECT OF ACIDIFICATION									
Paper no.	1			2 and 3				1			2 and 3			6			
Experiment	Colonisation experiment			Field experiment			Huhta et al.	Colonisation experiment			Field experiment			Birch leaves Field	Birch leaves Green-house		Bååth et al.
Additional information	Raw humus	Poor mull	Rich mull	A-1 1975	A-1 1977	A-3 1978	1983	Raw humus	Poor mull	Rich mull	A-2 1975	A-2 1977	A-3 1978		Early decomp.	Late decomp.	1980
2. Reduced abundance by acidification and/or increased abundance by liming.																	
ACARI																	
Oribatei																	
Chamobates sp. ad.															–		
Hemileius initialis Berlese, ad.															–		
Porobelba spinosa (Sellnick), ad. + juv.																–	
Steganacarus magnus (Nicolet), ad.	+																
Mesostigmata																	
Pergamasus lapponicus Trägårdh, ad.									–								
Veigaia nemorensis (C.L. Koch), ad. + juv.	+															–	
Trachytes sp. ad. + juv.					+								–		–		–
Uropodina, total													–				
Prostigmata																	
Prostigmata, total													–				
COLLEMBOLA																	
Isotoma notabilis Schäffer	(+)						+	(–)		–			–8)	–	–	–	
Isotomiella minor (Schäffer)			(+)							(–)			–		–	–	
Lepidocyrtus cyaneus Tullberg												–		–		–	
Onychiurus absoloni (Börner)							+						–1)				
Mesaphorura tenuisensillata Rusek		(+)							(–)								
Neelus minimus Willem															–		
PROTURA																	
Protura, total	(+)					+		(–)									
3. Reduced abundance recorded both by acidification and liming																	
ACARI																	
Mesostigmata																	
Parazercon sarekensis Willmann, ad. + large juv.						–						–	–				
COLLEMBOLA																	
Onychiurus armatus s.l. (Tullberg)			–			–							–		–		

Continues ÷

÷ Continued

	EFFECT OF LIMING							EFFECT OF ACIDIFICATION									
Paper no.	1			2 and 3				1			2 and 3			6			
Experiment	Colonisation experiment			Field experiment			Huhta et al.	Colonisation experiment			Field experiment			Birch leaves Field	Birch leaves Green-house		Bååth et al.
Additional information	Raw humus	Poor mull	Rich mull	A-1 1975	A-1 1977	A-3 1978	1983	Raw humus	Poor mull	Rich mull	A-2 1975	A-2 1977	A-3 1978		Early decomp.	Late decomp.	1980
4. Various reactions																	
ACARI																	
Oribatei																	
Brachychochthonius zelawaiensis (Sellnick), ad. + juv.	-				-	-1)			+					+	-		
Brachychthoniidae, total			-			-1)	-				+2)			+	-		
Oppiella nova (Oudemans), ad.	-							+							-	+	
Oppia obsoleta (Paoli), ad.			(-)							(+)							-
Oppia neerlandica (Oudemans), ad.							-										
Suctobelba sp. ad.						-1)	-		-	+			-1)				
Mesostigmata																	
Prozercon kochi Sellnick, ad. + large juv.	(-)							(+)								-	
Gamasina	(-)					-		(+)	-			-	-			-	
Mesostigmata, total	(-)					-		(+)	-			-	-			-	
Acari, total						-		+				+3)	-		+		
COLLEMBOLA																	
Friesea mirabilis (Tullberg)	(+)							(-)					+2)				
Collembola, total				-		-	-				+		-1)		-	-	

1) Sign. only in 0-3 cm layer. 2) Sign. only in 3-6 cm layer. 3) Sign. only in 4-6 cm layer. 4) Sign. only in 0-2 and 4-6 cm layer. 5) Sign. only in bleached layer (E). 6) The effect refers to pH 3-treated plots. 7) The effect refers to pH 2.5-treated plots. 8) A significant increase at the pH 4-treatment is probably a random variation. 9) Only ad. counted.

A. Species increasing their abundance following acidification and reducing their abundance after liming:

Tectocepheus velatus	(Oribatei)
Nothrus silvestris	»
Brachychochthonius zelawaiensis	»
Schwiebea cf. *nova*	(Astigmata)
Mesaphorura yosii	(Collembola)
Anurida pygmaea	»
Willemia anophthalma	»

B. Species increasing their abundance following liming and reducing their abundance after acidification:

Isotoma notabilis	(Collembola)

As shown in papers 9 and 10, the species in group A occur mainly in rather acid soils with a pH around 4 or below. *Isotoma notabilis*, however, achieves the highest abundance values in soils with a pH above 4. For all these species, the field studies support the hypothesis that their abundance is related to the soil acidity. Also literature data cited in the relevant papers give the same indications. Figure 1 illustrates the relatively good agreement between experimental studies and field studies for three of the most characteristic species (data from papers 1, 2, 3, 9, 10). While the experimental results have usually been related to treatments in the relevant papers, Figure 1 shows the abundance values directly related to soil pH in both experiments and field studies.

One difficulty when referring to older literature, is that methods for measuring soil pH vary, and in some papers the method is undescribed. For instance, measurement of soil pH in a KCl solution gives lower values than in a water suspension. However, literature data have been used only to confirm general patterns. Furthermore, in most of the papers referred to, the microarthropod fauna has been *compared* in soils with different pH levels, and the faunal trends which have appeared are in this connection more important than the exact values of soil pH.

Soil pH may vary seasonally and be influenced by drought periods. In papers 9 and 10, both spring and autumn faunal data are related to pH values measured in the autumn. However, compared to the pH-gradient in the material, seasonal pH variations would be small and would not change the major patterns between animal abundance and soil acidity level.

Of course soil acidity is only one of many factors modifying the abundance of these species, and the relation is not absolute. Even when the soil pH is suitable, other limiting factors, for instance drought, may depress the population. In several cases, the species in group A showed low abundance in certain very acid soils, for instance in the driest habitat (Cl-Pn) (Fig. 1). However, high abundance of these species has never been observed in soils of high pH.

The available information supports the following conclusion: for several species, high abundance can only be achieved within a certain pH interval (and only if other factors are not limiting), while within another certain pH interval, high abundance is never achieved. In soils of the latter pH interval, the acidity level (or correlated factors) seems to be limiting.

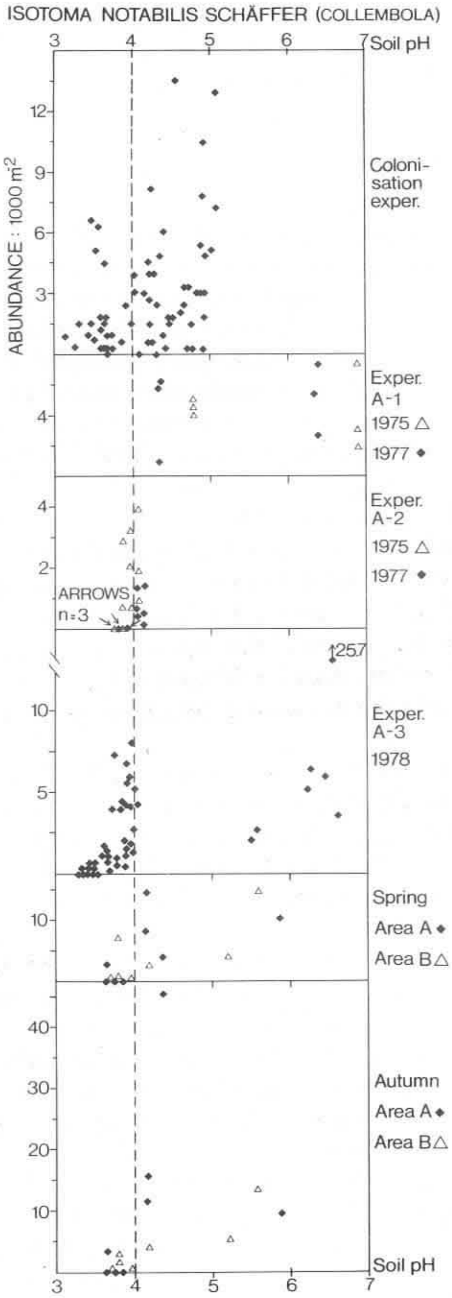
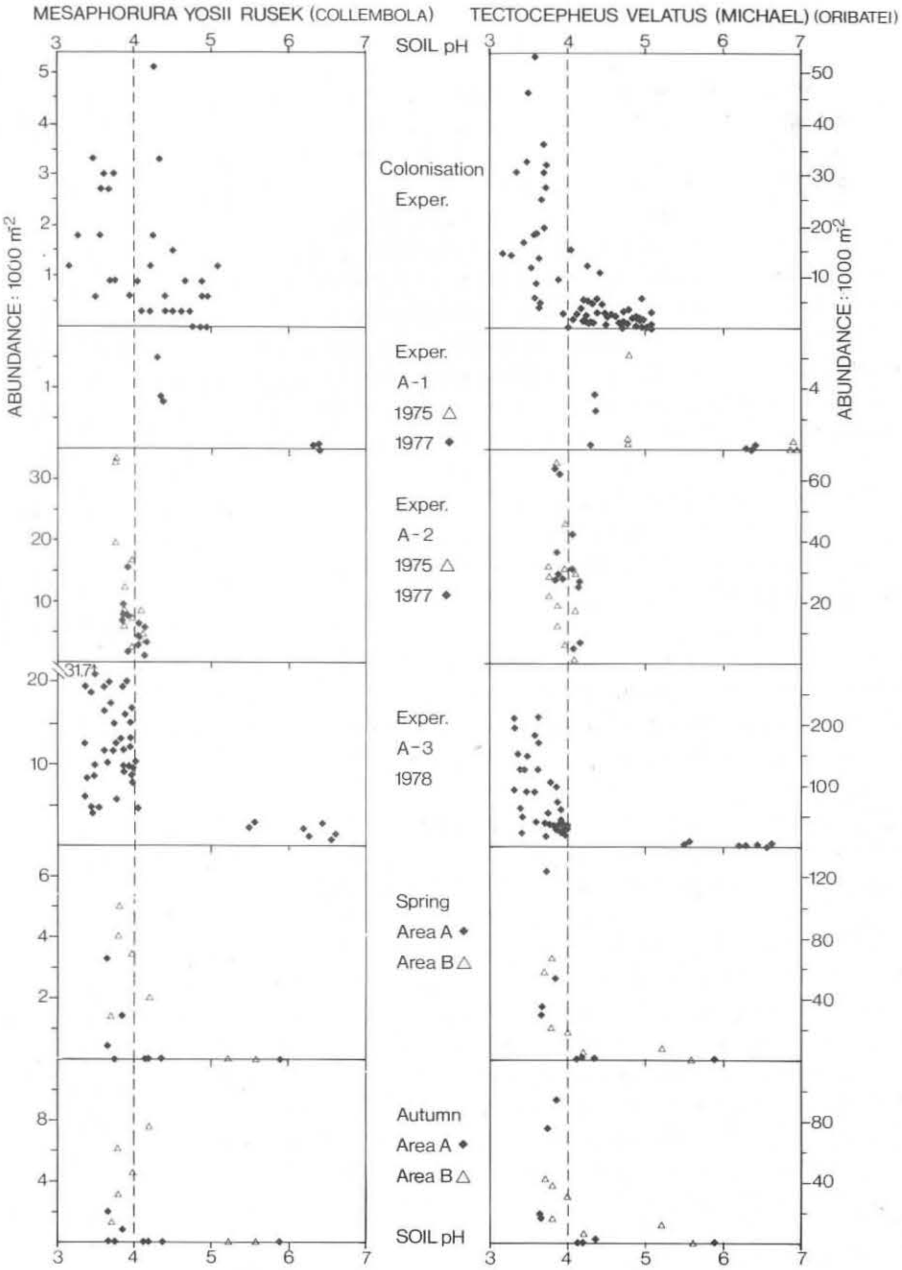


Fig. 1.

Relationships between soil pH and abundance of two Collembola and one Oribatei species. The »colonisation experiment» was described in paper 1. Experiments A–1, A–2, and A–3 were treated in papers 2–3. Field data (spring and autumn) were taken from different coniferous forests in SE Norway (paper 7). Except for the 1977 data in experiments A–1 and A–2, where the abundance values are from the 0–2 cm layer, all information is from the 0–3 cm layer. In the colonisation experiment, the sample size was 33.3 cm^2 (corresponding to one plot in the diagram), and the depicted data are from the raw humus soil. In experiments A–1, A–2 and A–3, one plot represents one replication, each replication being the mean of 10–14 soil cores of 5.3 or 10 cm^2. In the data from natural soils, each plot represents the mean of 20 soil cores, each 10 cm^2.


MESAPHORURA YOSII RUSEK (COLLEMBOLA)
TECTOCEPHEUS VELATUS (MICHAEL) (ORIBATEI)
SOIL pH
Colonisation Exper.
Exper. A-1 1975 △ 1977 ◆
Exper. A-2 1975 △ 1977 ◆
Exper. A-3 1978
Spring Area A ◆ Area B △
Autumn Area A ◆ Area B △
ABUNDANCE : 1000 m^{2}
31.7

2.4. Hypotheses

The observed relations between abundance and soil acidity are difficult to explain. Soil pH is a measure of the H^+ activity of the soil solution. It is reasonable that this parameter may be of direct importance to the water-living part of the soil fauna (such as Protozoa and Rotifera), and to other groups which live in extensive contact with the soil solution, for instance Nematoda (Bonnet 1961, Stachurska-Hagen 1980). Also Enchytraeide and Lumbricidae prefer relatively high moisture in the soil (Abrahamsen 1971 and 1972 a,b). Hågvar and Abrahamsen (1977) showed that the survival of the Enchytraeide species *Cognettia sphagnetorum* Vejdovsky decreased rapidly when the animals were submerged in diluted sulphuric acid of pH below four. Among Enchytraeidae, many species show distinct relations to soil pH, both in experiments and in the field (Abrahamsen 1972a, Hågvar and Abrahamsen 1980 (paper 1), Bååth et al. 1980, Abrahamsen 1983). The dependence of Lumbricidae species upon soil pH is well known (Satchell 1955, 1967, Abrahamsen 1972b, Nordström and Rundgren 1974).

Microarthropods are restricted to the air-filled pore spaces of the soil and have a hydrophobic cuticula. Most probably the relations found between abundance and soil pH are indirect, acting through factors or processes which are correlated with the acidity of the soil solution.

Several hypotheses may be proposed to explain the present results, and effort should be made to refute them. The combination of field- and laboratory studies, and natural versus manipulated soils, makes it possible to refute at least some of the hypotheses. A discussion of various hypotheses follows.

Hypothesis 1. The changes in the microarthropod fauna in the field experiments were indirectly due to the marked reduction of the ground vegetation (mainly the mosses) by the strongest treatments with sulphuric acid.

Comments: In the field experiments, significant changes in the microarthropod fauna occurred simultaneously with a marked reduction in the moss cover. However, similar faunal reactions to acidification were observed also in the colonisation experiment and the field experiment with birch leaves, where the samples lacked vegetation during the whole experiment. A special analysis of the abundance of *Parazercon sarekensis* in one field experiment showed a distribution independent of the moss cover at each treatment (paper 2). Generally, surface-living species were not more clearly affected by loss of the moss cover than deeper-living species. Differences in the amounts of living or dead roots in the samples might be important for the fauna, but a number of characteristic reactions were noted in the field experiment with birch leaves (paper 6), and very few roots had grown into these litter samples.

Hypothesis 2. The faunal changes in the liming and acidification experiments were not related to the soil pH changes as such, but more directly to the lime or sulphuric acid applied.

Comments: Similar relations between abundance and soil pH have been observed for several species in natural soils of different acidity (papers 9 and 10). In these soils, variations in soil pH were not brought about by extreme concentrations of the chemicals used in the experiments. Huhta et al. (1983) found that increased soil pH had the same effect on the microarthropod fauna, regardless of whether it was due to liming or to fertilizers.

Hypothesis 3. Observed relations in natural soils between pH and abundance of certain microarthropods are due to variations in factors correlated to soil pH, such as N-content, loss on ignition, humus type or soil profile (see papers 7, 9 and 10).

Comments: Similar faunal reactions to soil pH variations were observed in the liming and acidification experiments, where the factors mentioned above were insignificantly affected by the treatments. Certain soil chemical parameters are, however, always linked to the pH level of the soil (base saturation and the content of various base cations, mainly Ca).

Hypothesis 4. The increased abundance of certain microarthropod species in acidified samples is due to reduced predation pressure.

Comments: Microarthropods represent a suitable prey for several predators, especially the larger predatory Gamasina mites (Mesostigmata). Increased abundance of Collembola in DDT-treated soil has been related to reduced numbers of Gamasina (e.g. Sheals 1956, Edwards et al. 1967). The abundance of these Gamasina was, however, largely unaffected by acidification. Furthermore, the increase of potential prey species often occurred below 3 cm depth, while the relevant predators live mainly in the upper 3 cm layer. The possibility exists, however, that other predators are important, for instance certain egg-predators.

Hypothesis 5. The population changes were due to different food conditions at the various pH levels, especially the availability of fungal hyphae.

Comments: Fungal hyphae are found in the gut contents of many species, and are generally considered to be an important food item for microarthropods. Relations between microarthropods and the fungal flora are, however, difficult to study. The following considerations disimply a simple connection between changes in the fungal flora and the microarthropod fauna:

– No significant changes in the fungal biomass (FDA-active hyphae and total hyphae) occurred in one of the field experiments with artificial acidification, where characteristic changes in the microarthropod fauna were observed (see papers 2 and 3). Qualitative changes in the fungal flora, and hyphae production per unit time were, however, not studied.

– The species which increase their abundance in acidified soil or litter show large variations in ecology and morphology (size, depth distribution, mouthparts and gut contents). It is difficult to understand how certain changes in the fungal flora can affect these different species in the same way. Furthermore, various fungus-feeding species reacted differently to acidification (for example the common species *Isotomiella minor* was either unaffected or negatively affected by acidification, while another fungal-feeder, *Mesaphorura yosii*, often increased its abundance in acidified soil).

– Unpublished studies on the gut contents of *Mesaphorura yosii, Isotoma notabilis* and *Nothrus silvestris* from the colonisation experiment (paper1) did not reveal drastic effects of the treatments. Besides measuring to what degree each gut was filled, and the percentage of empty guts, the gut contents were divided quantitatively into the following fractions: fungal spores, dark hyphae, light hyphae, brown particles (unidentified), amorphous material, and mineral particles.

Hypothesis 6. The fecundity (egg production) of certain species is directly related to soil pH (for instance via food quality).

Comments: Preliminary counts of ripe and developing eggs within *Tectocepheus velatus* from different treatments in the colonisation experiment (paper 1) and the A-3 (1978) field experiment (paper 2) are difficult to interpret, but do not clearly support the hypothesis.

Hypothesis 7. The population growth rate of certain species is correlated with the soil acidity.

Comments: In several experiments with acidification and liming, it was found that microarthropod species which were especially common at a certain treatment, also had a high percentage of juveniles in the relevant samples. These observations led to the hypothesis that there is a correlation between soil pH and reproductive success in several microarthropods (papers 1 and 2). Also certain experiments and observations from the literature, referred to in the two first papers, support this hypothesis.

However, the observed high populations with a large fraction of juveniles can also be brought about by factors other than increased reproduction, for instance lowered mortality rates of eggs or juveniles.

An unpublished study was carried out to test hypothesis 7. In three species, which in several experiments had shown increased abundance in acidified soil and reduced abundance in limed soil, the population growth at different pH levels was studied. The species were *Mesaphorura yosii* (Collembola), *Schwiebea* cf. *nova* (Astigmata) and *Nothrus silvestris* (Oribatei). When kept in pure culture at different pH levels, each species' population growth could be related to the soil pH without being influenced by predators or interspecific competition. Raw humus samples were adjusted to different pH levels as described in paper 1. They were then sterilised with gamma radiation and inoculated with soil microflora (first by soil solution sieved through a nylon cloth with 5 μm mesh size, and then by letting soil fungi grow in through corresponding meshes for 1–2 months). All cultures started with twenty animals, and extractions were made after 3, 6 and 12 months. This study showed that the three species did not repeat their characteristic reactions to soil pH when they were alone. In several samplings, the trend was the opposite, i.e. largest populations developed in limed samples. On this basis, the hypothesis can be refuted.

These considerations lead naturally to the next hypothesis.

Hypothesis 8. Competition between species is a major population-regulating factor, and at different soil pH levels, different species are favoured in the competition process.

Comments: The culture experiments with single species referred to above indicate that the »characteristic» reactions to soil pH changes occur only in the presence of other faunal elements. Competition studies may therefore lead to fruitful information. Even in the »colonising experiment» (paper 1), where animals were allowed to colonise soil samples of different pH values, the establishment and development of the fauna in the samples occurred under continuous competition. The functional relations between various soil animals are, however, poorly known. The general reduction of Enchytraeidae on strongly acidified field plots (Abrahamsen 1983) could for instance have induced the observed increase of certain microarthropods, if these groups compete for essential resources. However, corresponding responses among microarthropods were observed in acidified soil in the colonising experiment, without any simultaneous reduction in Enchytraeidae (paper 1).

While competition may be a key word in explaining the observed results, the number of possible mechanisms is high. Several experimental approaches are probably needed.

At the present state of knowledge, some general considerations can be made. While it was stressed under hypothesis 5 that the species increasing in acidified soil showed considerable differences in ecology (including feeding habits), these species do in fact have one important feature in common: they all belong to the most dominant microarthropod species in the raw humus soils used in the experiments. The natural pH of these soils was about 4.0, so the pH must be characterized as rather low even before the artificial acidification started. As pointed out in paper 3, it is reasonable to assume that the factors initiating the increased abundance of these species during artificial acidification are the same factors which have induced their general high dominance in naturally acid soils. By increasing soil acidity the relevant species may thus be increasingly favoured in the competition process. If competition is strong, the highest abundance under field conditions may be achieved under quite another pH value than that proved to be the optimal pH in pure culture.

If hypothesis eight is correct, a general study of the competition factors for the relevant species in raw humus might lead to the explanation of increased success under even more acidic conditions.

2.5. Relations to acid precipitation

All significant reactions to artificial acidification were observed in treatments where the soil or litter pH had been changed, mostly after application of water of acidity pH 2.5 or pH 2. The limited number of replications in the field experiments implies, however, that only large changes in the animals' abundance could be discovered. The question remains therefore whether treatments with »weaker» acids (for instance pH 3 or 4) could induce faunal changes. It is also an open question whether possible faunal effects initiated by less acidic solutions would have the same character as the changes reported in the present studies.

It is difficult to decide whether acid precipitation has changed soil acidity yet, and whether this is probable in the long term. It depends for instance on the ability of the weathering rate to keep pace with the leaching rate of metal cations. Abrahamsen and Stuanes (in press) consider it reasonable that a slight reduction in soil pH may have occurred already in Norwegian soils.

In the present investigations, there was no consistent relation between the total abundance of microarthropods and the decomposition rate of raw humus and litter. Liming, and especially acidification, probably influence the microfloral activity to such a large degree (Bååth et al. 1979, 1980) that effects of faunal changes on decomposition become undetectable. In acidified soil, therefore, the total abundance of microarthropods cannot be used as an indication of decomposition rate.

3. Various aspects of microarthropod ecology

Below, abstracts are given for papers 5, 7 and 8. The following discussion focuses upon some selected items. One item covers the relationships between microarthropods and soil chemical factors other than pH. These relationships were described in connection with the »soil acidity» studies, and reference is made to the abstracts of papers 9 and 10 in chapter 2.1.

3.1. Abstracts

Paper 5. Succession, diversity and feeding habits of microarthropods in decomposing birch leaves.

Succession of microarthropods in decomposing birch leaves [mixture of *Betula pubescens* EHRH. and *B. verrucosa* EHRH.] was studied during a three-year period. The leaves were kept in litter bags under small *B. verrucosa* plants (0.5–1 m) on a clear-cut area with a podzol soil (Typic Udipsamment) in a Norway spruce/Scots pine forest. Litter bags were laid out 28.7.1975 and sampled on 19.9.1975, 28.4.1976, 2.–9.11.1976 and 10.11.1978. An intense immigration phase was observed. At the first sampling, the majority of all species recorded from bags over three years were already present, and the abundance was the highest in the study. However, more than half of the numbers were made up by only six »pioneer» species, belonging mainly to the litter fauna: three Oribatei [*Oribatula tibialis* (NICOLET), *Autogneta trägårdhi* FORSSLUND and *Eupelops duplex* (BERLESE)], two Collembola [*Entomobrya corticalis* (NICOLET), and *Lepidocyrtus cyaneus* TULLBERG], and one Astigmata [*Tyrophagus* cf. *fungivorus* (OUDEMANS)]. A second phase was observed during the later samplings, in which diversity increased and species characteristic for deeper layers took over the dominance. It was shown for several species that the changes in abundance and dominance were not due to their life cycle patterns, but probably reflected true successional changes. A third phase, in which the last rare species were invading the substrate, was believed to occur at the end of the study period.

A laboratory experiment indicated that when the habitat was saturated with species, a fourth phase occurred, in which the abundance was reduced in most species, but practically without changes in species composition. A fifth phase is predictable, in which both abundance and species numbers are reduced, as the resources are exhausted. Analysis of gut contents showed that all »pioneers» except *E. duplex* were typical microphytophages. All microphytophages studied ingested large amounts of fungal spores in the early decomposition phase, while fungal hyphae later became increasingly important. Practically all Collembola and Oribatei species in the surrounding soil invaded the birch litter, even though the litter type was atypical for the site. However, the relative dominance was different.

Paper 7. Collembola in Norwegian coniferous forest soils I. Relations to plant communities and soil fertility.

In each of two coniferous forest sites in SE-Norway, the soil-living Collembola fauna was investigated in seven different vegetation types. Soils ranged from poor podzol soils to rich brown earth. A total of 60 Collembola species were found. In all sites, a large fraction of the species (mean value 46%) were rare, with dominance values below 1%. In most soils, the fauna was quantitatively dominated by a few euryecious species (ecological generalists).

Species numbers increased with increasing soil fertility. Total abundance was highest in the second or third richest soils, while diversity was highest in medium rich soils.

Three species were common in all vegetation types. The main ranges of the other species varied greatly, but could in most cases be related to soil fertility. All vegetation types favoured some species.

Within each study area, soils near each other on the fertility scale (according to the vegetation types) showed a high similarity in the Collembola communities. However, due to differences in species composition between the two study areas, corresponding vegetation types might contain rather different Collembola communities. It is suggested that the more extreme the environmental conditions are (e.g. soil moisture), the better can vegetation indicate the Collembola fauna.

Paper 8. Collembola in Norwegian coniferous forest soils II. Vertical distribution.

The vertical distribution of Collembola was studied in seven different vegetation types in coniferous forest of SE Norway. Samples (down to 12 cm if possible) were taken in spring and autumn in two different study areas, each containing all the relevant vegetation types. The soils varied from poor and acid podzols with raw humus, to rich brown earths with mull humus.

The average depth of practically all species was situated in the upper 6 cm in all soils. In podzol soils, only four species (*Tullbergia callipygos, T. quadrispina, Karlstejnia norvegica* and *Wankeliella mediochaeta*) had their mean depth consistently below 6 cm, i.e. in the mineral layer. Except for the larger species restricted to the surface layers, many species showed considerable variation in depth distribution between both soils and seasons. Still, certain characteristic vertical distributions could be demonstrated for many species. A considerable overlap existed between hemiedaphic and euedaphic species. In most species, there was no consistent difference between mean depth in podzol and brown earth soils.

The relative vertical position of the different species (based on average depth) was rather flexible, between both soils and seasons. Certain relative positions were, however, never broken. A system of five depth levels, each with characteristic species, was recognized and described. A large number of factors probably influence the vertical position of a species. It is suggested that each species continually adjusts its vertical distribution in order to optimize its life and reproductive conditions.

This also implies that the community structure continually undergoes vertical changes. A single sample from a habitat gives only a transient picture of the Collembola fauna at different depth levels.

3.2. Ecological flexibility

If we shall try to make some general conclusions about the ecology of microarthropods in Norwegian coniferous forest soils, one of the most apparent features is the high ecological flexibility of many species, This implies that differences between communities (at least for Collembola) to a large degree can be described by changes in the dominance structure between species. The tolerance for various factors is further discussed below.

a) Substrate: Paper 7 showed that many Collembola species extend their distribution into quite different soil types and humus types, supporting various plant communities. There was no conspicuous change in the species composition between podzol soil and brown earth, or between raw humus and mull. Neither did the mite species studied in paper 10 (with the possible exception of an affinity of *P. sarekensis* to raw humus) show consistent relations to soil or humus type. The general flexibility of microarthropods regarding substrate is also documented in the study of paper 5, where practically all Collembola and Oribatid species in a coniferous podzol soil colonised samples of birch leaves. The colonisation of this unfamiliar substrate was probably due to favourable food conditions (a highly-productive and diverse microflora). Furthermore, most of the microarthropod species were represented, at least by some specimens, during all the relevant decomposition phases, where the substrate underwent significant changes.

The extensive geographical distribution of many microarthropod species reflects this large tolerance for various substrates. A gradual spread into new areas is, of course, highly facilitated if »barriers» of more extreme substrates can be tolerated, at least by some individuals. Also other studies, for instance by Bödvarsson (1961), have demonstrated the great habitat tolerance of several Collembola species.

b) Vertical distribution: Although each Collembola species can be assigned a certain »characteristic» depth interval, and several species seem to maintain constant vertical positions relative to each other (paper 8), flexibility is a key word also for the vertical distribution of this group.

The very sharp border between the O and E layers in the relevant podzol soils did not give a correspondingly marked change in the Collembola fauna, neither in species composition nor in numbers. For many species, considerable variations in vertical position were observed both between different habitats, and between spring and autumn in the same site. Such variations were

observed even for the six mite species studied in paper 10.

The data in paper 8 clearly demonstrate that one sampling gives only a transient picture of the vertical distribution of the Collembola fauna. Leinaås (1976) demonstrated seasonal changes in the vertical position of many Collembola species during a year. Evidently, the vertical flexibility makes it possible to survive adverse periods of cold or drought, while for instance the upper layers can be recolonised during favourable conditions, when an actively growing microflora in the O_1 and O_f layers may represent a valuable food source. Each species thus continually adjusts its vertical position to optimize its survival and reproductive ability. A more rigid vertical separation of the species could temporarily reduce the interspecific competition, but would be a disadvantage for many species as soon as adverse or favourable conditions develop in certain layers.

c) Food choice: The well-known fact that many Collembola species can be cultured when fed brewer's yeast indicates a great flexibility in the food choice of these animals. In a literature review, Petersen (1971) concluded that the varying information about food preferences and gut contents in Collembola can be explained if we assume that each species constantly selects the best food items from what is available in the given situation. The present results from paper 5, showing that many species of Collembola and Acari change their food habits through the different successional stages, are in good accordance with the observations of Anderson (1975). Clearly, much more information must be collected about the food habits of microarthropods from different substrates, successional phases, probably depth levels, and even seasons (cf. Anderson & Healey 1972) before a system about feeding categories can be completed. A further challenge is to clarify the nutritional value of the different food items, including studies of enzymes in the guts of various species. Here lies a key to understanding more completely the functional role of microarthropods in the decomposition processes.

3.3. Relations between plant communities and Collembola communities

A close relation between plant communities and Collembola communities could have two possible bases. Either plants and animals react in a parallel way to the same environmental factor(s) (as for instance soil moisture), or the Collembola might be sensitive to factors initiated by the various types of vegetation (litter composition, root systems, etc.). The lack of a good correlation between the Collembola fauna and vegetation types, as described in paper 7, shows that plants and

Collembola are to a high degree regulated by different environmental factors, and the floral composition does not have any decisive regulating effect on the composition of the Collembola community.

A complicating factor in the study was that the Collembola fauna in each study area tended to have a local character. Very often, a Collembola community showed greatest similarity with that of another vegetation type in the same area. Pure geographical distance seems to be a factor of considerable importance in Collembola. In various European grassland soils, Wood (1966) found that the species compositions of Collembola, Mesostigmata and Oribatei were more similar in different soils from the same locality than in different localities. In the succession study (paper 5), the colonising fauna differed markedly within distances of 20–50 m in an apparently homogeneous area. As discussed in paper 7 (p. 291), a commonly distributed ubiquitous species may be locally absent. In addition to historical factors, one factor which may play a major role for Collembola is the microflora. This and other factors may theoretically vary within an apparently homogeneous vegetation type. It is, however, even possible that interspecific competition and the use of pheromones may create local variations in the structure of Collembola communities even within an homogeneous area.

Nonetheless, there is a very broad relation between Collembola communities and the level of soil fertility. This relation is even better if each study area is treated separately. There is also a general correlation between plant and Collembola communities in either very dry or very moist sites. Evidently, extreme soil moisture conditions give characteristic reactions among both plants and Collembola.

The above considerations imply that for coniferous forest soils, the ground vegetation is more suited than the Collembola fauna to indicating soil types and fertility levels.

3.4. Relations between microarthropods and soil chemical factors other than pH

The relationships found between certain soil chemical data (other than pH) and the abundance of some microarthropod species should be further tested in other soil types. Several soil chemical factors can be intercorrelated, and correlations may also appear by chance without any functional basis.

In general, microarthropods seem to have few strong relations to soil chemical parameters. As these animals live in the air-filled cavities of the soil, they have only limited contact with the soil solution, and they will probably only in indirect ways be affected by soil chemical parameters. It is, however, reasonable that certain broad relations exist, partly because of the dependence of the microflora upon several chemical factors, and because chemical factors may be correlated with structural and physical properties which are of importance for these small, pore-dwelling animals. From papers 7 and 10, it was evident that the main distribution of many microarthropods could be broadly related to the level of soil fertility (expressed through tree growth).

3.5. Indicator value of Collembola

Only some of the relevant Collembola species seem to have so specific environmental requirements that they deserve the title of »indicator species» in coniferous forest. The following species and environmental factors should be mentioned:

a) Soil moisture: Four species were characteristic for dry sites (*Anurophorus septentrionalis, Isotoma sensibilis, Xenylla boerneri,* and *Hypogastrura inermis*). One species, *Isotoma olivacea*, occurred mainly in moist soil. As referred to in paper 7, these conclusions conform well with earlier studies.

b) Depth level: While most of the large, pigmented species are well-known inhabitants of the uppermost O-layers (for instance *Isotoma hiemalis, I. viridis, Lepidocyrtus lignorum, L. cyaneus* and *Anurophorus septentrionalis*), many species show a rather large flexibility in the vertical distribution. Only four species had their mean vertical position consistently below 6 cm depth: *Tullbergia callipygos, T. quadrispina, Wankeliella mediochaeta* and *Karlstejnia norvegica.* If one species characteristic for medium depth levels shall be selected, the common *Anurida pygmaea* can be used, having its mean depth level around 6 cm depth in most soils (see paper 8).

c) Soil pH: From chapter 2.3, we note that *Mesaphorura yosii, Anurida pygmaea,* and *Willemia anophthalma* achieved high abundance only in rather acid soils (with pH around 4.0 or lower), while *Isotoma notabilis* was abundant only in soils with higher pH levels.

From paper 5 it also appears that the dominant species may indicate the level of decomposition in a certain substrate, as the pioneer species are recruited from the litter fauna, while deeper-living species dominate later. The approximate fertility level of a coniferous forest soil can also probably be deduced from the total Collembola fauna (paper 7). A high abundance of a specific species may indicate seve-

ral features of the soil. For instance, a soil sample from coniferous forest which contains high mumbers of *A. pygmaea* indicates a rather acid, medium rich soil. The soil moisture would probably also have a medium character. In addition, the sample indicates a depth level of 3–9 cm.

3.6. Some general characteristics of the Collembola fauna of coniferous forest soils in SE Norway

Apart from in the driest and wettest habitats, the Collembola fauna was usually dominated by very common and euryecious species. *Isotomiella minor* was the most abundant species in seven of the fifteen habitats. Changes in the community from one site to another were to a large degree due to dominance changes between species. This may indicate that interspecific competition is strong, and that different dominance patterns are stable under different environmental conditions. Clearly, species lists alone represent a poor basis for describing different forest Collembola communities.

The high fraction of rare species is another characteristic feature of the Collembola communities, which is also confirmed by other studies in Scandinavian coniferous forest sites (paper 7). This reservoir of rare species will prove to be still larger if more intensive studies are performed. As pointed out in paper 7, they represent a valuable genetic reserve, and they strengthen the general impression of flexibility in these Collembola communities. Small »islands» of special soil or environmental conditions in a forest landscape should have a good chance of aquiring a »characteristic» Collembola community by immigration of selected species from the nearest surroundings.

The distribution of each Collembola species in the various forest types can often be related to soil fertility. Also similarities in community structure are on a large scale related to soil fertility. The study has not indicated any direct connection between certain plant species and certain Collembola species. The most species-rich Collembola communities were, however, found in the most fertile soils, which supported the highest number of plant species.

The present studies showed that detailed analysis of the species complex »*Tullbergia krausbaueri*» was rewarding. Several closely related parthenogenetic species, identified on the basis of chaetotaxi, seem to be ecologically separated (papers 1, 7 and 8).

Preliminary investigations of the Collembola fauna of special soil microsites and above-ground habitats have revealed several species not found in the ordinary soil cores of »typical» patches of the relevant forest types. Collembola can clearly be used to illustrate adaptations to very different microhabitats in forest ecosystems.

3.7. Aspects of succession

Studies of succession processes are of basic ecological interest. Because they are easy to sample, have a high number of species and short generation time, microarthropods are very well suited for successional studies. The phases described in paper 5 (and in earlier papers referred to) should be further tested, and late phases of the process should be included. Effort should be taken to exclude non-successional population changes due to seasonal or year-to-year variations.

The intense immigration phase observed in paper 5, dominated by a few »pioneer species», represents an interesting phenomenon. Food conditions are clearly very good in this early phase, and abundant food may allow many species to coexist in a substrate with a low structural diversity. As the »pioneer species» were rare in ordinary soil samples, the rapid concentration of these species in the litter bags may have been due to smell stimuli from the substrate or microflora, or even the use of pheromones by the relevant species. These aspects ought to be further studied.

Paper 5 showed that there are various local alternatives in the faunal changes during the succession. However, the fauna starts with a litter fauna and gradually changes to a community characteristic for deeper layers. Since the vertical position of the leaves did not change during this study, the species expressed real preferences for different decomposition phases of the substrate. This aspect may be further analyzed by preference experiments in the laboratory.

Studies of gut contents in dominant species throughout the various phases of succession are helpful in trying to understand the faunal changes. Studies of age distribution would probably also be fruitful. The observations in paper 5 indicated that several species did not reproduce in the substrate, but only visited it during the adult stage for feeding purposes. The dynamics of microarthropods in decomposing substrates may generally shed light upon several aspects of microarthropod ecology, including competition and limiting factors for species numbers and population size.

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